

Establishment and spread of founding populations of an invasive thistle: the role of competition and seed limitation

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Abstract Successful plant invasions require both the founding and local spread of new populations. High plant densities occur only when founding plants are able to disperse their seeds well locally to quickly colonize and fill the new patch. We test this ability in a 7-year field experiment with *Carduus acanthoides*, an invasive weed in several North American ecosystems. Founder plants were planted in the center of 64 m² plots and we monitored the recruitment, distribution pattern, mortality, and seed production of the seedlings that originated from these founding plants. Competing vegetation was clipped not at all, once, or twice each year to evaluate the importance of interspecific competition. More seedlings recruited in the intermediate once-clipped plots, and these seedlings also survived better. The control plots had fewer microsites for seedling recruitment; clipping

a second time in September stimulated grasses to fill up the gaps. The number of *C. acanthoides* recruits and their median distances from the founder plants were also explained by the initial seed production of the founding plants. Overall, the experiment shows that the success of founder plants can fluctuate strongly, as 55% of the plots were empty by the sixth year. Our study suggests that the local invasion speed following initial establishment depends strongly on both the propagule pressure and availability of suitable microsites for seedling recruitment and growth.

Keywords *Carduus acanthoides* · Founding populations · Invasion · Microsite limitation · Neighborhood expansion · Propagule pressure · Seed limitation · Stratified diffusion · Weed

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Introduction

Biological invasions can be described by stratified diffusion: new populations are founded by long-distance dispersal, after which these founders colonize the new site in a wave like fashion (Hengeveld 1989; Andow et al. 1990; Shigesada and Kawasaki 1997). Thus, invading weeds need not only the capacity to disperse over long distances but also the ability to rapidly increase in population density when they colonize a new area (Pauchard and Shea 2006). However, invaders are

often studied in existing populations (e.g., Shea and Kelly 1998; Lambrecht-McDowell and Radosevich 2005). Unfortunately, populations of fugitive biennials are ephemeral, and thus most established populations will show population declines (van der Meijden et al. 1992). A better understanding of the dynamics of newly establishing populations is essential, and may provide insight into control options in the important early stage of invasion.

The successful establishment of a population after arrival in a new site (Kolar and Lodge 2001) is limited by several factors that can affect either the recruitment or the growth of new plants. Some of these factors have to do with the plant and some with the environment (Shea and Chesson 2002): production and dispersal of seeds, the availability of suitable microsites at the time of recruitment (Eriksson and Ehrlén 1992; Jongejans et al. 2006b), and interspecific competition by neighboring plants (Fenner 1978). These factors together determine the invasion wave speed with which a weed colonizes a new site (Schippers et al. 1993; Kot et al. 1996; Neubert and Parker 2004).

Here, our objective was to investigate how initial propagule pressure and above-ground competition affect the establishment success of a new population. We study the recruitment and resultant distribution patterns of the progeny of founder *Carduus acanthoides* plants during the initial colonization phase of an invasion. This invasive thistle is a major pest in the USA, where it can form dense infestations. Its wind-dispersed seeds (Feldman and Lewis 1990) and association with man-made habitats enables this species to invade most of temperate America, but it is found to have low competitive abilities in established vegetation, as it needs gaps for recruitment (D. Ruggiero, E. Rauschert, and K. Shea, unpublished results). Here we therefore test the ability of *C. acanthoides* to spread locally under three different levels of interspecific competition by clipping the surrounding vegetation not at all, once, or twice, to simulate different competition regimes.

Materials and methods

Plumeless thistle, *C. acanthoides* L. (Asteraceae), is a European thistle that has invaded pastures,

right-of-ways and natural areas throughout the temperate USA. It was first recorded in the USA in 1879 (Desrochers et al. 1988). A survey by Dunn (1976) reported infestations of *C. acanthoides* in 188 counties in 19 states; by 2002 it had been reported in 31 states (Allen and Shea 2006). In Maryland, only one county was originally listed as infested (Dunn 1976), but at least nine counties were infested by 1999 (P.W. Tipping, unpublished data). In some of those counties, Tipping (1992) reported infestations of more than 15,000 plants per ha in permanent pastures. The monocarpic rosettes of *C. acanthoides* can potentially form flower stalks up to 2 m high before they die. It reproduces strictly by seed, which can be dispersed by wind using its attached pappus (Feldman and Lewis 1990; O. Skarpaas and K. Shea, submitted for publication).

This study was conducted for 7 years (1993–1999) at the Maryland Department of Agriculture facility in Cheltenham, MD. The site was a slightly rolling 8 ha field with no recorded history of *C. acanthoides*. The soil series was a combination of sandy loams (types Keyport and Matapeake) and clayey, mixed, mesic soil (Aguic Hapludult) with a 2% slope. The study area was dominated by the grasses *Andropogon virginicus* L., *Festuca arundinacea* Schreb., *Dactylus glomerata* L. and *Cynodon dactylon* (L.) Pers., that were routinely mowed prior to this study. A 0.2 ha area was plowed up and disced in July 1993 as *C. acanthoides* is expected to colonize especially well after vegetation disturbances. The field was divided into 24 plots, each 8 m × 8 m with a 1 m wide border. Rosettes (52 ± 9.7 cm mean diameter and standard deviation) of *C. acanthoides* were planted individually in the center of each plot on October 11, 1993. These plants served as the experimental “founder” plants for evaluating a population that was invading a new patch. The experimental layout was a randomized complete block design with three treatments over eight blocks. These treatments consisted of clipping all vegetation that re-established in the plots during the first year after plowing, except all *C. acanthoides* rosettes, never (control), once (usually in July), or twice (in July and September) each year from 1994. By clipping the vegetation in the plots we simulated conditions where the

thistles experience less above-ground competition and seeds encounter more gaps for recruitment, such as in pastures (the thistles are not eaten by cattle) or mowed right-of-ways. Please note that the July clipping was done in the main flowering period of *C. acanthoides*, while no seeds were produced in September. Clipping was done with a rotary mower throughout the entire plot and with hand clippers around thistle plants to avoid damaging them, at an approximate height of 7–8 cm. Border margins were never mowed. No attempts were made to exclude any organisms that may affect various life stages of the plant, such as generalist predators like rodents, birds, ants, or more specialized insect herbivores like the three Coleoptera: *Cassida rubiginosa* Müller (Chrysomelidae), *Rhinocyllus conicus* Froelich and *Trichosiocalus horridus* (Panzer); the latter two are members of the Curculionidae.

The flowering heads in the experiment were counted each week. A head was considered in flower if any corolla tubes with color were visible. Seed dispersal usually occurred 7–10 days later. To non-destructively estimate the number of seeds produced by the flower heads in the experimental plots on a weekly basis, 25 greenhouse-grown rosettes of *C. acanthoides* were planted in an adjacent plot each fall, starting in 1993. These extra plants were arranged in a square grid with 92 cm between the plant centers. All mature heads were sampled up to three times per week before seed dispersal and returned to the laboratory where seeds were removed and tested for germination (Tipping 1991).

Seed bank estimates were made once on March 29, 1995, by sampling along transects radiating outward from the founder plant in eight directions at distances of 2.5, 15, 31, 61, and 92 cm for a total of 40 samples per plot. A soil corer sampled an area of 5.1 cm² to a depth of 7.6 cm and soil cores were bulked within distance and plot. Previous studies in *C. acanthoides* infested areas with well-established soil seed banks in western Maryland found that more than 97% of seeds occurred within 7.6 cm of the soil surface (P.W. Tipping, unpublished data). Samples were pulverized and spread in a thin layer over a bed of ProMixTM in individual flats and placed in a greenhouse under ambient conditions. Flats were watered as needed

and seedlings of *C. acanthoides* were recorded and removed until no more germination occurred. Samples were then lightly stirred when no new seedlings were detected after 2 weeks. Three cycles of stirring were done and sampling was discontinued after the last stirring, because of the low probability of detecting new germinations.

All individual seedlings, rosettes, and bolted plants in the experiment were recorded, numbered, and marked with flags 1–4 times each year (18 October 1994, 28 March, 15 June and 1 December 1995, 11 April, 14 June and 24 September 1996, 27 March, 18 June, 22 September and 17 December 1997, 1 April, 22 June, 23 September and 15 December 1998, and 21 April 1999). The numbers of different individual plants in a plot observed during at least one census in a year were used in the analyses. The distance from the founder plant in the center of the plot to recruited plants was measured to the nearest centimeter.

Data analysis

We analyzed the fate of the founding population in 1998 (any plants present or not) as a function of initial seed production and the clipping treatments in a generalized linear model with quasibinomial error distribution. The effects of these factors on the total number of recruits over the years in a plot (log-transformed after adding 1 to increase normality of the data) and on the median distance of all recruits in a plot were analyzed with ANCOVAs. The trends (over the years) in the numbers of rosettes and seeds produced per plot were studied with generalized linear mixed models, with quasipoisson error distribution, that accounted for the fact that the same plots were studied each year (Pinheiro and Bates 2000). The trends in distances of the new recruits from the plot center were analyzed with a similar model but with normal error distribution, after normalizing the data by log-transformation. Finally, we calculated expansion speeds for each treatment × year combination as the ratio of the 90-percentile of the distances of new recruits in that year, to the number of years since the founder plants released their seeds. All analyses were done in R (R Development Core Team 2005).

Two plots (with only one recruit each) were left out of all the analyses because we suspected inter-plot seed dispersal: in those two plots (a 1× clipping plot and a no clipping plot) a rosette appeared near the border more than a year after the last seed production event in those plots. In both cases the seedling appeared after an interval in which plants in adjacent plots produced seeds. In other plots in which seedlings appeared from the seed bank, they always appeared closer to the center.

Results

All of the founder plants bolted, flowered and produced seeds in 1994, with the peak of seed rain in the second week of July. The number of seeds produced by the founder plants (1111 ± 614 mean and standard deviation, $n = 22$) was not significantly different among blocks ($df = 7$, $MS = 120 \times 10^3$, $F = 1.66$, $P = 0.18$) or treatments ($df = 2$, $MS = 83.9 \times 10^3$, $F = 0.947$, $P = 0.41$), as was to be expected since the treatments were only initiated once the founder plants were flowering. However, for the next 2 years the average seed rain was low (59 and 233 seeds per plot, respectively), before increasing in 1997 (especially in the single clipping treatment: 3541 seeds per plot; Table 1). Despite the similar initial quantity of seed rain in the plots, neither

seedlings nor rosettes were detected in four of the plots from the spring and summer of 1995 to the spring of 1999. In another eight plots none of the recruits produced seeds before dying. The clipping treatment affected the total number of plants present in the plots during the later part of the study with significantly larger numbers found in the plots that were clipped once annually (Tables 1 and 2). Generally, if one recruited seedling was able to survive and produce seeds, then more recruitment was likely in subsequent years, especially if many seeds were produced. Without regular infusions of seeds to the soil seed bank, thistle populations went to zero within 2–4 years in this study, suggesting that the soil seed bank was not long-lived. Furthermore, the soil seed bank sampling in March 1995 yielded only one seedling at the 15 cm interval from the founder plant out of 320 samples. These results agree with those of Roberts and Chancellor (1979) and Feldman and Lewis (1990) who characterized the soil seed bank of *C. acanthoides* as transient. By 1998, 55% of the plots were empty of *C. acanthoides* (Fig. 1).

The number of seeds produced by the founder plants had a significantly positive effect on whether or not any *C. acanthoides* rosettes were present in a plot in 1998 (Fig. 1, $t = 2.25$, $P = 0.037$), with more occupied plots in the once clipped group ($t = 1.74$, $P = 0.098$) than in the no clipping group. The total

Table 1 Demographic statistics of the founder plants and their offspring

Variables	No clipping		1× clipping		2× clipping	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
<i>Seed production per plot</i>						
1994	1420	231	1037	168	905	247
1995	0	0	186	186	0	0
1996	88	88	400	400	214	214
1997	582	290	3541	2446	0	0
1998	18	12	1982	1409	2	2
<i>Number of rosettes per plot</i>						
1994	1.1	0.1	1.1	0.1	1.5	0.5
1995	2.4	1.4	2.6	0.6	1.3	0.6
1996	4.9	2.3	2.4	1.0	1.0	0.6
1997	5.1	2.9	4.1	1.3	0.1	0.1
1998	1.3	0.7	11.3	7.2	0.9	0.6
Recruit mortality (%)	59		49		63	
Bolting by surviving recruits (%)	28		19		18	
Seed production bolting recruits	248		1880		855	

See Table 2 for statistical tests on the plot-level differences in rosette number and seed production. The individual mortality, bolting and seed production rates are averages of all individuals that were found in all plots within a certain treatment over the years

Table 2 Results of general linear mixed models of total seed production and rosette number per plot with quasipoisson error distribution, and of the log-transformed distances (to the plot center) of the recruits with normal error distribution

Parameter	Seed production			Number of rosettes			Distance of recruits		
	Effect	df	<i>t</i>	Effect	df	<i>t</i>	Effect	df	<i>t</i>
Intercept	7.48	85	11.67***	0.27	85	0.48	– 2.35	210	– 16.75***
1× clipping	– 1.96	19	– 2.27*	– 1.18	19	– 1.45	0.27	210	2.56*
2× clipping	0.43	19	0.40	0.31	19	0.36	– 0.24	210	– 1.52
Year	– 0.61	85	– 2.42*	0.10	85	0.90	0.47	210	12.93***
1× clipping × year	1.00	85	3.58***	0.47	85	2.97**			
2× clipping × year	– 0.65	85	– 1.13	– 0.36	85	– 1.60			

The 1× clipping and 2× clipping parameters in the models denote their deviation from the no clipping treatment. The year and clipping interaction had no significant ($P > 0.69$) effect on the recruit distances and therefore no interaction was included in that model. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

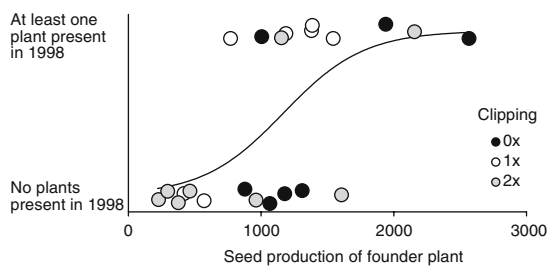


Fig. 1 Presence or absence of any *C. acanthoides* plants in a plot in the 6th year (1998) of the clipping experiment. Dots are spread out vertically for visual clarity

number of recruits in a plot over the years was also significantly explained by initial seed production (Fig. 2, $df = 1$, $MS = 5.35$, $F = 4.79$, $P = 0.042$) and showed a trend with the clipping treatments ($df = 2$, $MS = 3.24$, $F = 2.90$, $P = 0.081$) with higher numbers in the once-clipped plots. The

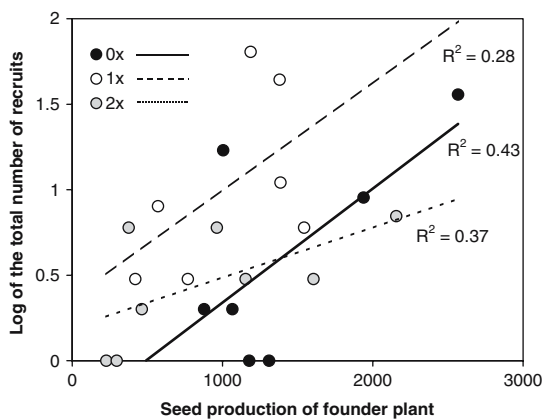


Fig. 2 Relationships between the total number of recruits in a plot over the years with the clipping treatment and the seed production of the initial plant in that plot. Rosette numbers were $\log(x + 1)$ transformed

interaction term was not significant ($P = 0.80$) and was omitted from the model. Together, initial propagule pressure and clipping still account for only a moderate part of the variation in the number of recruits ($R^2 = 0.37$). Mortality was not affected by the clipping treatments (Table 1), but was affected by season: the greatest percentage of the recruited population died during the summer followed by winter, spring, and the fall. Smaller rosettes that were recruited during the spring were particularly vulnerable to desiccation during periods of drier weather and warmer temperatures that occurred during their first summer. For example, a summer drought killed many rosettes in 1998.

The pattern of recruitment was heavily concentrated around each flowering plant, usually within the periphery of the branches, but more distant seedling recruitments occurred as well.

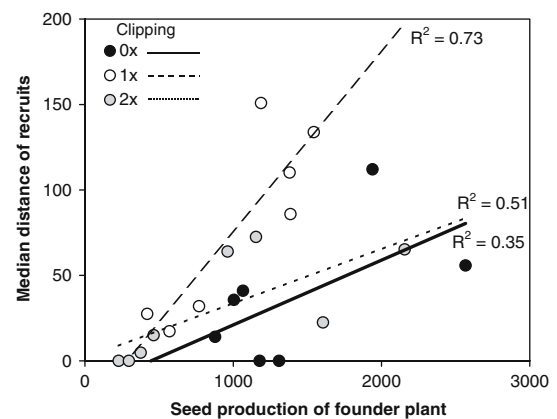


Fig. 3 Relationships between the median distance from the center of all new plants in a plot over the years, with the clipping treatment and the seed production of the initial plant in that plot

The median recruitment distance increased with founder plant fecundity (Fig. 3, $df = 1$, $MS = 136 \times 10^2$, $F = 14.9$, $P = 0.0014$), but more so for the once-clipping treatment than for the two other treatments (clipping: $df = 2$, $MS = 5161$, $F = 5.65$, $P = 0.014$, interaction: $df = 2$, $MS = 2883$, $F = 3.15$, $P = 0.070$). The recruitment distances were higher in the once-clipped plots throughout the duration of the experiment (Fig. 4,

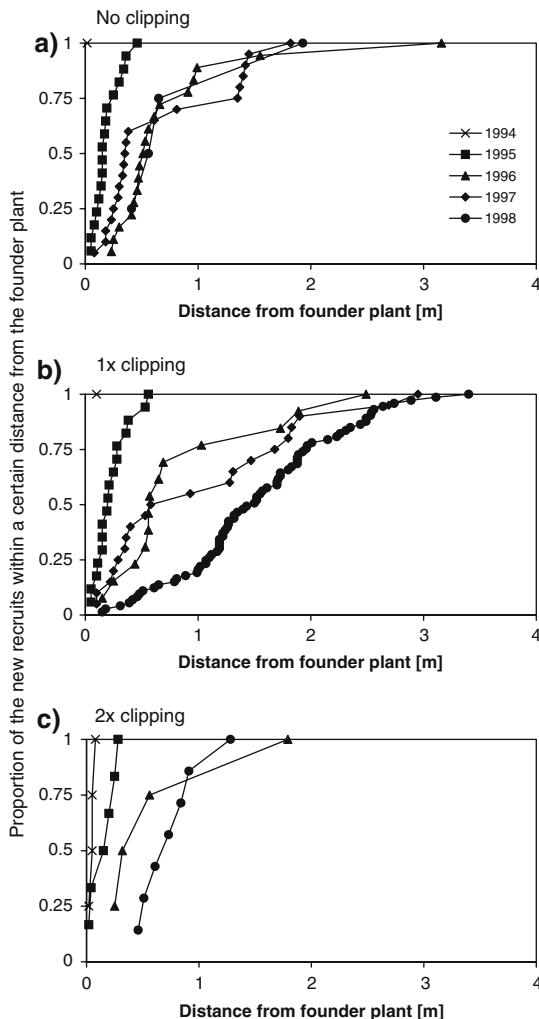


Fig. 4 Proportion of the new recruits within a certain distance [m] from the founder plant, separately for each clipping treatment and year. In 1994, the year in which the founding plants produced seeds, only one recruit was found in all unclipped plots (a), one in the 1× clipped plots (b) and four in the 2× clipped plots (c). No new recruits were found in the 2× clipped plots in 1997. The last year of the study, 1999, is not included in these diagrams because the plots were not monitored the whole year. See Table 2 for statistical details

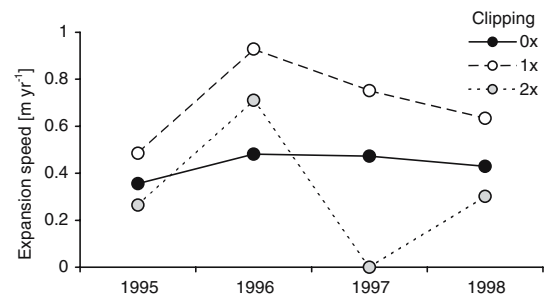


Fig. 5 Expansion speeds calculated for each year × clipping treatment combination as the ratio of the 90-percentile of the distances of new recruits in that year, to the number of years since initial seed production

Table 2). No recruits were detected further than 3.5 m from the center of the plots, while the maximal distance within the plots was 5.7 m (i.e. from the center to a corner), although the distances above 4 m had lower detection probabilities because they occurred only in the corners of the square plots. The invasion wave speeds that resulted from these dispersal distances were moderate: on average 0.43, 0.70 and 0.32 m year⁻¹ in the unclipped, once-clipped and twice-clipped plots, respectively (Fig. 5).

Discussion

High seed production of the founder plant and removal of aboveground competitors resulted in the largest thistle invasions. Once-clipped plots with high initial seed production contained more recruited plants and these were further away from the founder plant. Management that removes the vegetation while leaving the thistles intact, such as grazing, therefore clearly facilitates local invasion of *C. acanthoides*. In the unclipped plots there was a preponderance of grasses with clumped or bunched growth habits that strongly contrasted to the mown grass in the two other clipping treatments (P.W. Tipping, personal observation). The timing of the clipping was also important. Clipping when seed rain was underway likely increased, at least temporarily, the number of available microsites. However, this advantage was nullified in plots clipped again in the fall by stimulating growth, clonal propagation and germination of cooler season grasses, like *Bromus*

species, which either closed microsites or out-competed thistle seedlings. Below we discuss the consecutive steps of colonization: seed production and dispersal, seed arrival at suitable microsites, and the survival and growth of the new recruits.

Seed production

Our results show clearly that the invasion success rate and invasion wave speeds increase with the seed production of the founder plant. This is in accordance with theoretical models of invasions (Kot et al. 1996; Shigesada and Kawasaki 1997), and empirical studies of the importance of propagule pressure (Veltman et al. 1996; Memmott et al. 1998). Several specialist insect species have been used as biological agents to reduce the seed production of *C. acanthoides* and the congeneric *C. nutans* (Shea and Kelly 1998; Kok 2001), but these insects were mostly absent in our experiment. Specialist herbivores that cause seed losses probably would have a large impact on the population establishment success of founder plants, but such specialists are rarely present at the inception of a novel invasion.

Seed density on the soil

At the earliest stage of this experimental invasion, numerous gaps were still present after plowing. It is therefore likely that the *C. acanthoides* populations were initially seed limited. Post-dispersal seed predation by generalist predators may have caused seed losses, as many studies on post-dispersal seed herbivory have recorded losses approaching 100% (Crawley 1992). Pre- but also post-dispersal seed predators were an important factor in reducing the seed bank and population growth rate of *C. nutans* in its native habitat (Sheppard et al. 1989; Jongejans et al. 2006a). Since our results also indicate that the seed bank is not very persistent, regular arrivals of new seeds are needed to utilize new microsites.

Microsite availability

As the experimental site aged and vegetation gaps closed, further recruitment may have

become microsite limited. Colonizing species like *C. acanthoides* are often poor competitors. In pastures most recruitment in *C. acanthoides* occurs in larger gaps (Feldman et al. 1994; Ruggiero and Shea, submitted for publication). The treatment designed to reduce interspecific competition the most in our experiment appears to have had the opposite effect because, as stated above, the second clipping in late summer or early fall may have promoted increased tillering and germination of grasses rather than creating more microsites for *C. acanthoides* seedlings.

In our study the recruitment success was greater closer to parent plants. Thompson et al. (1987) and Kelly et al. (1990) found that thistle seedlings were more likely to recruit in close proximity to thistles that bolted and died. This may be the result of predator satiation, of leaving a physically open gap, or of allelopathic protection provided by the parent plant. Wardle et al. (1993) found some evidence that *C. nutans* was allelopathic as extracts of thistle tissues stimulated conspecific seedlings and slightly reduced the germination of other pasture species, but research on the allelopathic status of *C. acanthoides* is still ongoing.

Recruitment distributions

The recruitment patterns in our experiment indicate strongly that the seeds were not dispersed uniformly, but that short-range dispersal was prevalent in our 8 m × 8 m plots. This is in agreement with observed seed dispersal patterns of this species (Feldman and Lewis 1990) and with the observation that its occurrence is regionally aggregated (Allen and Shea 2006). Stuckey and Forsyth (1971) and Wardle et al. (1991) found that many thistle seeds were not dispersed by wind but remained in the seed heads after they desiccated and fell off the plant. However, that does not mean that dispersal over longer distances does not occur. Our experiment was designed to study local patch filling by founder plants and not to quantify longer distance dispersal events. The two cases of likely contaminations from neighboring plots suggest that seed dispersal beyond the plot borders occurred occasionally. In dispersal experiments using

individually released *C. acanthoides* seeds Skarpaas and Shea (submitted for publication) found dispersal distances up to 52.6 m, while about 90% of the seeds did not exceed 8 m in a grazed field. In higher vegetation, long-distance dispersal was even less frequent.

Rosette survival and growth

Sheppard et al. (1989) found that rosette mortality of *C. nutans* in pastures was 90% in the summer because of drought conditions and poor soil fertility. We also found strong seasonal effects for *C. acanthoides*, with highest mortality in summers. Although the treatment effects on mortality were not significant the average mortality was lowest in the once clipped plots. This effect was significant, however, when only small rosettes (diameter < 19 cm) were considered, indicating that the same competitive factors affect thistle recruitment and the survival of small thistle rosettes.

Conclusions and implications for control

The expansion speeds, which we calculated as the annual increase in the 90-percentile front distance of the new recruits in the populations, are relatively small: maximally 93 cm year⁻¹. However, these neighborhood expansion speeds (Hengeveld 1989; Shigesada and Kawasaki 1997) are not directly comparable to regional invasion speeds that involve long-distance dispersal by wind (Skarpaas and Shea, submitted for publication) or by other means: the experimental design only allowed for quantification of the local population spread and did not allow for long-distance colonization of new populations. The observed low expansion speeds may be enhanced when gap-creating disturbances occur more intensely. On arable land cultivation machinery has been shown to strongly increase local wave speeds of weeds (Schipper et al. 1993; Bischoff 2005).

Interspecific competition in combination with seed limitation in the early stages is thus the central explanation for the absence of thistle outbreaks in most plots. The lack of establishment of longer-term thistle populations in 55% of the plots is consistent with the metapopulation dynamics of fugitive biennials (van der Meijden

et al. 1992). Klinkhamer et al. (1988) found that 51% of the local population of *Cirsium vulgare* went extinct over a 3-year period. Pre- and post-dispersal seed predation may have importantly affected the earlier stages of colonization of the disturbed site as well: the populations were seed-limited, as can be deduced from the fact that the founder's seed production is correlated with the number of recruits 6 years later.

Nevertheless, 45% of the founder plants did establish a population. The conditions in this experiment are likely similar to those at the time of the initial invasion into the USA (few specialist herbivores, grazed pastures with low thistle propagule pressure); *C. acanthoides* was first recorded in 1879 in New Jersey (Desrochers et al. 1988). Clearly this is a species that has a high probability of establishment and persistence. Given that this species was likely introduced frequently as a contaminant of agricultural seeds from Europe, its invasion success was assured.

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